SPATIAL PATTERNS, ENVIRONMENTAL CORRELATES, AND POTENTIAL SEASONAL MIGRATION TRIANGLE OF ARCTIC COD (*BOREOGADUS SAIDA*) DISTRIBUTION IN THE CHUKCHI AND BEAUFORT SEAS

By

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Abstract

Arctic Cod (*Boreogadus saida*) is a key forage fish species in the Arctic marine ecosystem and provides a critical energetic link between lower and upper trophic levels. Despite its ecological importance, spatially explicit studies synthesizing Arctic Cod distribution across a multitude of research efforts previously have not been conducted in the western portion of its range. I used spatial generalized additive models (GAM) to map the distribution of Arctic Cod by size class and relative to environmental variables. I compiled demersal trawl data from 21 research cruises conducted from 2004 to 2017 in the Chukchi and Beaufort seas, and investigated size-specific patterns in distribution to infer movement ecology of Arctic Cod as it develops from juvenile to adult life stages. High abundances of small, juvenile Arctic Cod (≤70 mm total length) in the northeastern Chukchi Sea and western Beaufort Sea were separated from another region of high abundances in the eastern Beaufort Sea, near the US and Canadian border, suggesting possible population structure in the Pacific Arctic. In both the Chukchi and Beaufort seas, large, adult Arctic Cod (>130 mm total length) were found offshore and spatially segregated from small and medium (71–130 mm total length) fish, indicating an ontogenetic offshore movement of Arctic Cod as it matures. Relating environmental correlates to Arctic Cod abundance demonstrated that temperature and salinity were related to juvenile distribution patterns, while depth was the primary correlate of adult distribution. Furthermore, a comparison of spring and summer 2017 abundances of Arctic Cod in the southern Chukchi Sea, from the Bering Strait to Cape Lisburne found low abundance in the spring when compared to the summer. Differences in Arctic Cod abundance at different times of year suggest that Arctic Cod migrate seasonally,

potentially following patterns of biological production in the Chukchi Sea. Arctic Cod migration may follow a classical ‘migration triangle’ route between nursery grounds as juveniles, feeding grounds as subadults, and spawning grounds as adults, in relation to ice cover and seasonal production in the Chukchi Sea. The analysis presented here is necessary to address federally mandated research requirements, which include improving understanding of stock structure and resolving essential fish habitat (EFH) for different life stages, as well as to gain better general understanding of the role of Arctic Cod in the Pacific Arctic.

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Introduction

The extreme environment of the Arctic marine ecosystem makes it both a rich source for scientific inquiry and a challenging location for study. Research conducted in this environment has historically been sporadic (Hopcroft and Day 2013), and it is only in the past several decades that an increase in industrial interest for resource extraction, shipping, and the potential for commercial fisheries has resulted in a concomitant increase in scientific study of the area. Currently, understanding of the basic life history of many marine organisms in the Arctic is based on intermittent "snapshots" of species' presence, abundance, and distribution. Arctic Cod is one such fish species that merits further research attention. While the distribution and movement of Arctic Cod has been investigated in Atlantic Arctic regions such as the East Greenland shelf (Astthorsson 2015), and the Barents, Laptev, and East Siberian seas (Ponomarenko 1968; Lønne and Gulliksen 1989), a comprehensive study synthesizing multiple research efforts to describe the distribution of Arctic Cod has yet to be completed for its range in the Pacific Arctic in the Chukchi and Beaufort seas (Mueter et al. 2016). Accordingly, it is critical to develop a holistic understanding of Arctic Cod distribution in the Chukchi and Beaufort seas and to explore patterns in distribution with respect to fish size.

Arctic Cod is an abundant, circumpolar forage fish species and plays a key role in the Arctic marine ecosystem (Lowry and Frost 1981; Mecklenburg et al. 2011; Hop and Gjosaeter 2013). This small-bodied Arctic species spawns under sea-ice in the late fall and early winter, and has buoyant eggs that float to the ice-water interface (Graham and Hop 1995; Bouchard and Fortier 2011). In the Pacific Arctic, Arctic Cod is found in high salinity and intermediate water temperatures of the Chukchi Sea shelf (Norcross et al. 2010; De Robertis et al. 2017b; Logerwell et al. 2017). In the Beaufort Sea, Arctic Cod is ubiquitous, present at all depths both on the shelf and extending seaward down the slope (Benoit et al. 2008; Geoffroy et al. 2011; Norcross et al. 2017). This abundant and widely distributed species forms a critical link between lower and higher trophic levels within the Arctic ecosystem (Welch et al. 1992; Whitehouse et al. 2014). Arctic Cod consumes zooplankton such as copepods, hyperiid amphipods, and euphausiids (Rand et al. 2013; Gray et al. 2016), and is consequently consumed by larger marine vertebrates such as birds, seals, and whales (Bluhm and Gradinger 2008; Harter et al. 2013). By facilitating the flow of energy through the food web, the presence of Arctic Cod as a trophic link is essential for the functioning of Arctic marine ecosystems.

Body size and ontogeny influence the ability of fishes to exploit available resources and may affect their distribution with respect to these resources. As fish size increases, individuals become stronger swimmers and can exploit larger and more energetically valuable prey resources (Werner and Hall 1974; Christensen 1996; Clark et al. 2005). As gape size increases with fish growth, the maximum size of prey that can be consumed also increases; a larger gape size does not exclude the consumption of smaller prey, thus widening the size range of exploitable resources (Scharf et al. 2000; Gray et al. 2017). In the Chukchi and Beaufort seas, body size is the most important factor in determining the complexity and composition of prey in Arctic Cod diets (Walkusz et al. 2013; Gray et al. 2016). Smaller Arctic Cod individuals are restricted to consuming smaller prey, such as calanoid and cyclopoid copepods, while larger individuals can also consume larger zooplankton, such as hyperiid amphipods and euphausiids (Gray et al. 2016; Norcross et al. 2017). Therefore, ontogeny and the associated increase in fish size influences the ability of Arctic Cod to exploit more resources and may affect its distribution with respect to these resources in the Pacific Arctic.

Differential distribution in fish size with respect to resources can influence species-level life history strategies, including both ontogenetic and seasonal migration patterns. In classic 'migration triangle' theory, species migrate from nursery grounds, to feeding grounds, and finally to spawning grounds throughout the course of a life cycle (Harden Jones 1968; Secor 2002). Many species in the North Pacific exhibit this life history strategy, including the close relatives of Arctic Cod, Pacific Cod (*Gadus macrocephalus*) and Walleye Pollock (*Gadus chalcogrammus*) (Shimada and Kimura 1994; Kotwicki et al. 2005). In addition to ontogenetic migrations, seasonal migrations are also common for fish species in the highly seasonal North Pacific ecosystem. Pacific Herring (*Clupea pallasii*) and Yellowfin Sole (*Limanda aspera*), for example, exploit abundant food resources as they migrate between summer feeding grounds and offshore overwintering grounds (Nichol 1998; Tojo et al. 2007). The migration patterns of Arctic Cod in the Pacific Arctic, either ontogenetic or seasonal, are not well established. Sampling October – June, in addition to August and September, when sampling typically occurs in the Chukchi Sea, could improve understanding of Arctic Cod seasonal migration patterns.

Global attention has recently shifted to the Arctic and its potential to provide ecosystem services for human use. An increasing human presence in the Arctic will undoubtedly alter the ecosystem. However, national and international fisheries management organizations will have the unique opportunity to incorporate precautionary management strategies for potential Arctic fisheries from the outset. For example, in 2009 the North Pacific Fisheries Management Council (NPFMC) closed US Arctic waters to commercial fishing until sufficient information becomes available to sustainably manage a fishery (NPFMC 2009), and a similar international fishing moratorium agreement was reached in 2016 and updated in 2018 by the "Arctic Five plus Five," countries that either neighbor or have an interest in Arctic waters (Hoag 2017; Hill 2018). Within the NPFMC Arctic Fisheries Management Plan, Arctic Cod is listed as one of only two finfish species with commercial potential, a classification that emphasizes the need for additional study of this species. To meet the research requirements stipulated by the NPFMC prior to fishery development, which include a review of the life history of the potential target species, as well as an evaluation of the potential impacts to essential fish habitat, it will be necessary to characterize the spatial distribution of Arctic Cod. While a number of recent pelagic and demersal trawl surveys conducted by both the National Marine Fisheries Service and academic researchers (Rand and Logerwell 2010; Norcross et al. 2013; De Robertis et al. 2017b) have described broad patterns in Arctic Cod distribution and overall abundance, as well as general Chukchi Sea fish community composition (Logerwell et al. 2015), a study specifically investigating Arctic Cod distribution patterns across multiple years and many cruises has yet to be completed. Accordingly, I generated a comprehensive understanding of Arctic Cod distribution in the Chukchi and Beaufort seas and investigated whether patterns differ by size class of fish. I also related environmental covariates to abundance to explore potential correlates of described Arctic Cod distribution. Finally, seasonal differences in Arctic Cod abundance in the southern Chukchi Sea were used to inform a hypothesis about an Arctic Cod migration triangle and the role of seasonality on Arctic Cod distribution.

Methods

Study Region

Within US waters, Arctic Cod is abundant in the Chukchi and Beaufort seas, two waterbodies with differing physical and biological conditions. The Chukchi Sea has a wide and shallow shelf with average depths ranging from 40 to 60 m. This sea benefits from an inflow from three primary water masses, nutrient poor Alaska Coastal Water (ACW), nutrient rich Bering Shelf Water (BSW), and nutrient rich Anadyr Water (AW) (Figure 1; Weingartner 1997; Weingartner et al. 2013; Danielson et al. 2017). There is considerable mixing between the BSW and AW, creating a water mass that has been termed Bering Chukchi Summer Water (BCSW) (Danielson et al. 2017). The ACW, BSW, and AW originate in the Bering Sea and travel northward through Bering Strait, transporting nutrients and creating areas of high primary production and rich benthic habitats in portions of the Chukchi Sea (Dunton et al. 2005; Grebmeier et al. 2006). The high levels of Chukchi Sea shelf productivity are influenced to a greater extent by nutrient input from BCSW, than by ACW (Grebmeier et al. 1988). In contrast to the Chukchi Sea, the Beaufort Sea has a much narrower shelf with a slope that drops off steeply to the Arctic Basin. In addition to nutrient-rich waters flowing eastward from the Chukchi Sea, oceanographic processes in the Beaufort Sea are influenced by water from the Atlantic Ocean, the Beaufort Gyre, and freshwater input from the Mackenzie River (Carmack and Macdonald 2002). Water masses in the Beaufort Sea include a continuation of the eastward flowing ACW from the Chukchi Sea, Summer Shelf Water (SSW) influenced by both sub-Arctic and Arctic currents, and deep Atlantic Water (AtlW) transported west from the Atlantic Ocean (Carmack et al. 1989; Lansard et al. 2012;

Norcross et al. 2018). Without nutrient subsidies from richer sub-Arctic waters, production in the Beaufort Sea is much lower than in the Chukchi Sea (Dunton et al. 2005). Regional differences in production create an unequal availability of resources between the Chukchi and Beaufort seas, which may drive both broad-scale patterns of Arctic Cod distribution between the two seas, as well as more fine-scale patterns of Arctic Cod distribution by size class in each respective sea. For this reason, all analyses were conducted separately for the Chukchi and Beaufort seas.

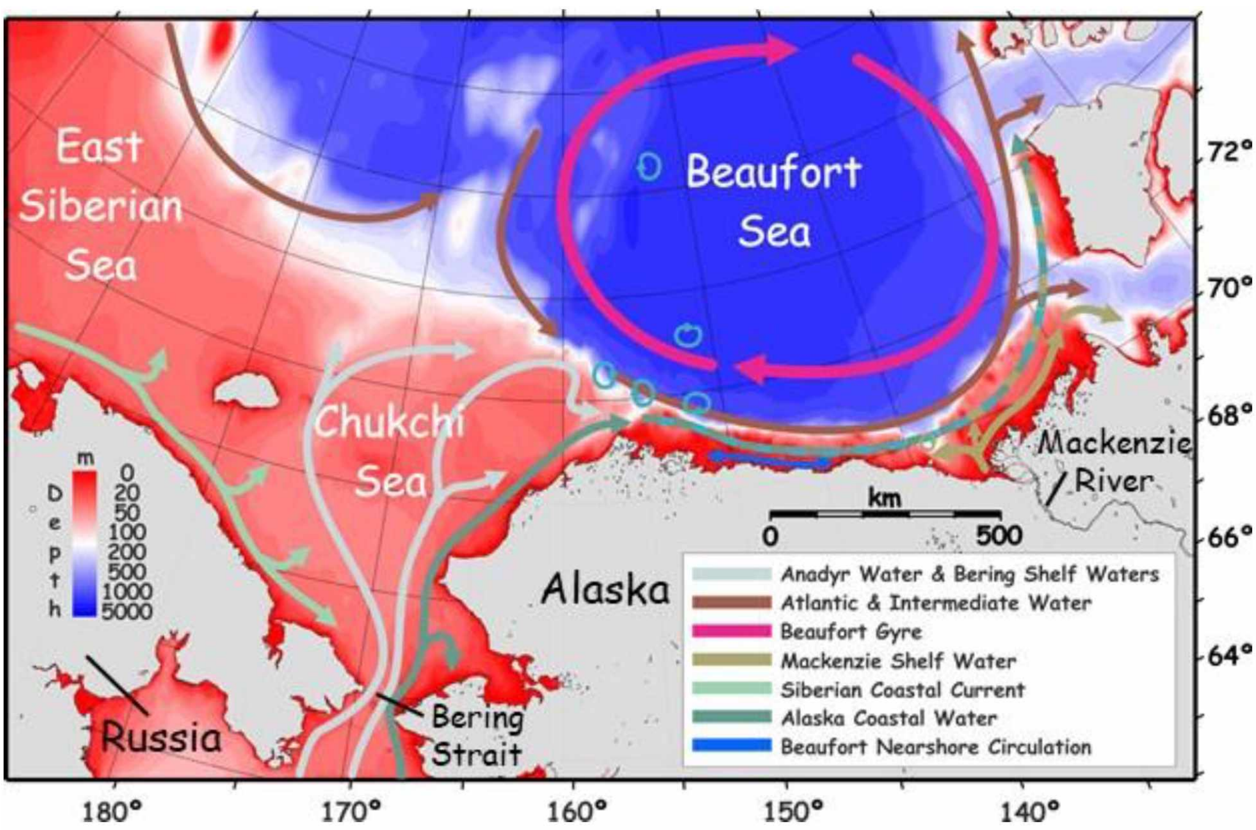

Figure 1. Schematic of oceanic current flow in the Chukchi and Beaufort seas. After S. Danielson, personal communication.

Data Collection

Data were compiled from 21 research surveys that were conducted during the open-water season in the Chukchi and Beaufort seas beginning in 2004 and extending through 2017. Data were available from 16 cruises in the Chukchi Sea and five cruises in the Beaufort Sea (Table 1). In the Chukchi Sea, station locations ranged from approximately 170 °W to Point Barrow, 156 °W, and from the Bering Strait, 66.4 °N, to approximately 73 °N. Because the Chukchi Sea is relatively shallow, sampled depths were commonly between 40 and 60 m, with a maximum depth of 90 m. Station locations in the Beaufort Sea extended along the Alaskan coast from Point Barrow and into Canadian waters past the Mackenzie River to 137 °W, and offshore to approximately 72 °N (Figure 2). Sampled depths reached nearly 1,000 m in the Beaufort Sea. Cruises were divided in to two seasons, spring and summer, based on date of sampling. A cruise conducted from 9 June to 29 June 2017 in the Chukchi Sea (ASGARD, Table 1), produced some of the earliest seasonal sampling events to ever take place in this region and was categorized as a spring season cruise. The remaining 20 cruises, conducted from 7 July to 10 October were categorized as summer season cruises. Because sampling in the spring occurred much earlier than during other cruises, data from this season were excluded from a spatial analysis of the summer distribution of Arctic Cod.

Table 1. Cruise information for all surveys used in this study listed by cruise designator, vessel used, year, beginning date of sampling, ending date of sampling, and number of hauls collected. Due to difference in sampling seasons, ASGARD_2017 cruise excluded from spatial analysis.

Region	Cruise Designator	Vessel	Year	Begin Date	End Date	No. of Hauls
Chukchi	RUSALCA_2004	R/V Professor Khromov	2004	10-Aug	22-Aug	5
Chukchi	OD0710	R/V Oscar Dyson	2007	4-Sep	15-Sep	21
Chukchi	OS180	T/S Oshoro-Maru IV	2007	6-Aug	10-Aug	9
Chukchi	OS190	T/S Oshoro-Maru IV	2008	7-Jul	13-Jul	15
Chukchi	COMIDA_2009	R/V Alpha Helix	2009	27-Jul	11-Aug	30
Chukchi	RUSALCA_2009	R/V Professor Khromov	2009	4-Sep	29-Sep	7
Chukchi	WWW0902	R/V Westward Wind	2009	14-Aug	29-Aug	25
Chukchi	WWW0904	R/V Westward Wind	2009	29-Sep	10-Oct	26
Chukchi	AKCH10	R/V Norseman II	2010	21-Aug	4-Sep	30
Chukchi	WWW1003	R/V Westward Wind	2010	1-Sep	18-Sep	40
Chukchi	AKCH11	R/V Norseman II	2011	4-Sep	17-Sep	28
Chukchi	Arctic EIS_2012	F/V Alaska Knight	2012	14-Aug	18-Sep	40
Chukchi	RUSALCA_2012	R/V Professor Khromov	2012	27-Aug	16-Sep	5
Chukchi	AMBON_2015	R/V Norseman II	2015	11-Aug	3-Sep	68
Chukchi	Arctic IES_2017	R/V Ocean Starr	2017	1-Aug	28-Sep	59
Chukchi	ASGARD_2017	R/V Sikuliaq	2017	9-Jun	29-Jun	8
Beaufort	BOEM_2011	R/V Norseman II	2011	15-Aug	4-Sep	81
Beaufort	TB_2013	R/V Norseman II	2013	12-Aug	2-Sep	90
Beaufort	ANIMIDA_2014	R/V Norseman II	2014	29-Jul	10-Aug	29
Beaufort	TB_2014	R/V Norseman II	2014	14-Aug	2-Sep	68
Beaufort	ANIMIDA_2015	R/V Norseman II	2015	31-Jul	8-Aug	18
					Total No. of Hauls	697

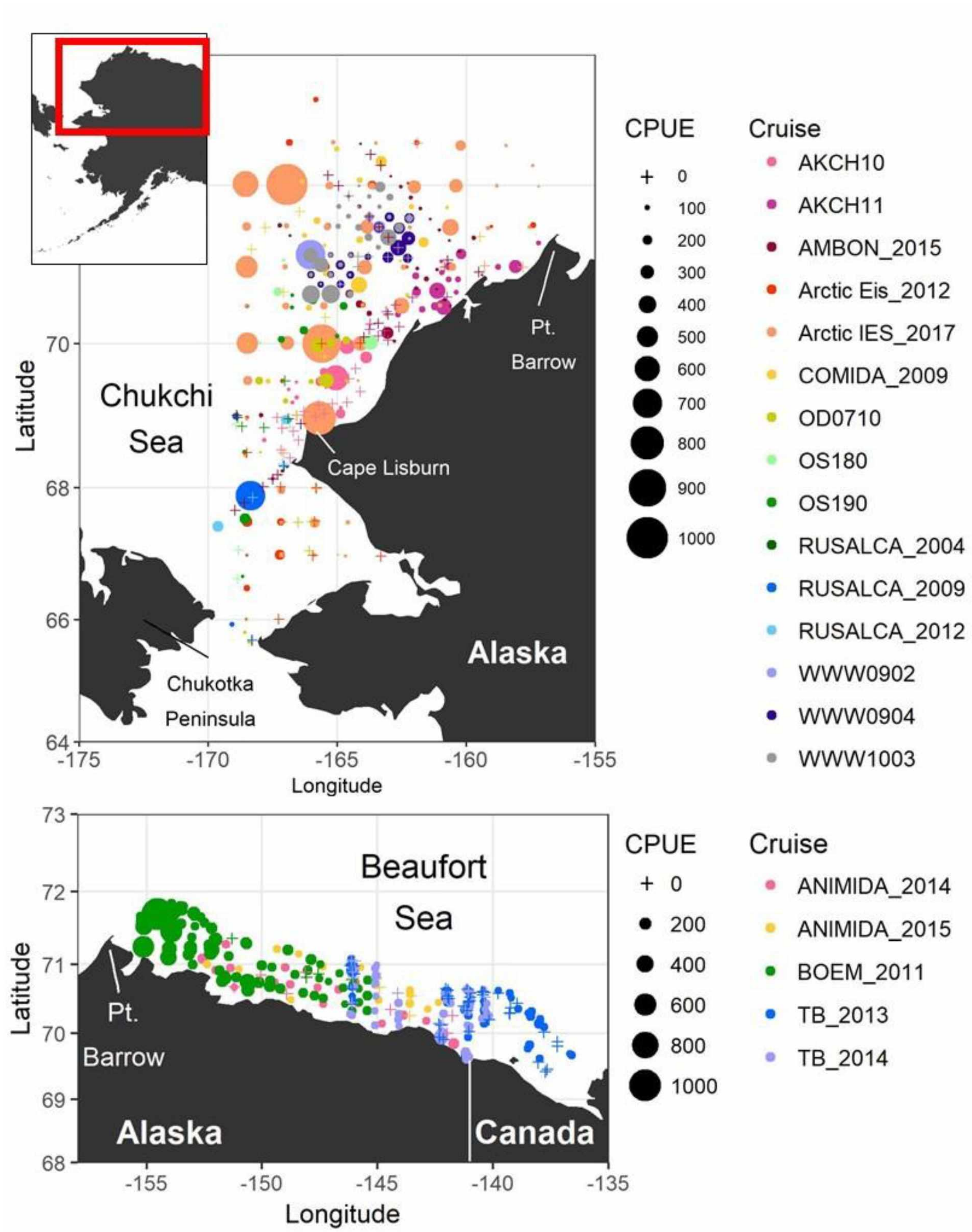

Figure 2. Catch per unit effort (CPUE, no. of fish per 1,000 m^2) of Arctic Cod by haul in the Chukchi Sea (top panel) and Beaufort Sea (bottom panel). The + symbol denotes hauls where zero Arctic Cod were caught. Colors correspond to separate cruises. For details about each cruise, see Table 1.

All Arctic Cod were captured in one of two configurations of a 3-m plumb staff beam trawl (PSBT), either standard (Gunderson and Ellis 1986) or modified with rollers (Abookire and Rose 2005), which were deployed for 1 – 10 minutes. A rigid 3.05 m beam held the net open for an effective swath of 2.26 m; net mesh size was 7 mm in the body with a 4 mm codend liner. In a gear comparison study, neither catch per unit effort (CPUE) of all fishes nor size classes of Arctic Cod were significantly different between these two gear types (Norcross et al. 2018), therefore, abundance data from both gear types were pooled for analysis. Fishing effort for each haul was defined as the total seafloor area swept by the net. Catches were standardized to an area of 1,000 m^2 (Catch per unit effort or CPUE in no. of fish per 1,000 m^2). In addition, at each haul location a Seabird conductivity-temperature-depth (CTD) recorder was deployed from the vessel separately and used to measure depth (m), bottom water temperature (°C), and bottom water salinity (PSU), hereafter referred to as depth, temperature, and salinity. Fish specimens were frozen and returned to the Fisheries Oceanography Lab at the University of Alaska Fairbanks for processing, where they were measured for total length.

Data Analysis

Patterns in Arctic Cod abundance and total length were plotted and inspected prior to statistical analysis. Length frequencies of 6,519 and 2,752 fish in the Chukchi and Beaufort seas, respectively, were plotted by 10 mm increments (1–10 mm, 11–20 mm, etc.) and examined to inform selection of size classes for analysis (Figure 3). Visual inspection suggested the presence of three modes, therefore size classes were identified using an expectation-maximization (EM) algorithm to fit a mixture of three Gaussian distributions to the length-frequency data (Benaglia et al. 2009). Based on the results, abundances of Arctic Cod were separated by total length into small (<70 mm), medium (71–130 mm), and large (>130 mm) size classes. Size classes approximately correspond with age 0, 1, and 2+ Arctic Cod, respectively, based on previously published work (Helser et al. 2017). However, given considerable overlap in length-at-age distributions, the medium size class likely contains a mixture of age 1 and age 2 individuals

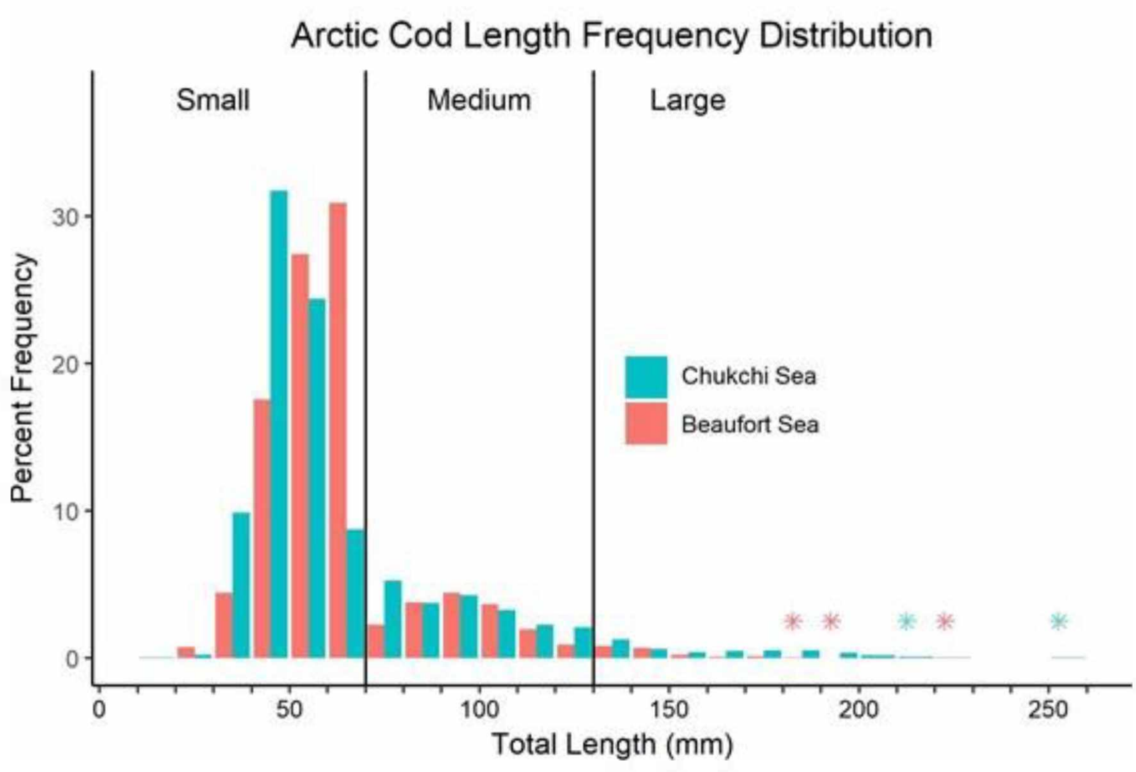

Figure 3. Length frequency distribution of Arctic Cod captured in Chukchi Sea (blue) and Beaufort Sea (pink), weighted by station-specific catch per unit effort (CPUE, no. of fish per 1,000 m^2). Percent frequency is percent of total CPUE for that sea, bars for size class in between tick marks. Asterisks above a length bin indicate percentage <0.1%, color corresponds to sea.

Generalized additive modeling (GAM) was used to relate CPUE of Arctic Cod to spatial and environmental predictor variables. A GAM is a regression technique that uses non-parametric smoothers to allow non-linear relationships between dependent and independent variables (Hastie and Tibshirani 1986; Wood 2006). The GAM approach was chosen to accommodate non-linear relationships between abundance and both spatial (latitude, longitude) and environmental (depth, temperature, salinity) predictors. All models were fit using the 'mgcv' package version 1.8-17 (Wood 2006) in R version 3.4.1 (R Core Team 2017).

To determine the most appropriate model framework for both the spatial and environmental GAM analyses, preliminary analyses and model diagnostics were conducted prior to selection of final models. Abundance of Arctic Cod was non-normal, including a high proportion of zero-catch hauls, as well as a few hauls with very high abundance values. Exploratory analyses compared models using a Gaussian distribution with log-transformed Arctic Cod CPUE and the identity-link function, with negative binomial and tweedie distributions using counts of Arctic Cod and the log-link function. The negative binomial distribution with a log-link was selected as the top performing model based on residual diagnostics, deviance explained, and generalized cross validation scores. This model framework was thereafter used for all GAM analyses. The negative binomial distribution utilizes count data, and is commonly used for analyzing ecological data, as it can accommodate overdispersed observations, or observations with a high proportion of zeros (Zuur et al. 2007). I used raw counts in the analysis and accounted for fishing effort by including the logarithm of area swept (m^2) as an offset in the model.

GAM analyses were conducted on cruises conducted in the summer season. Only T/S Oshoro-Maru IV 2008 (Table 1) was conducted early in the summer season, in July. To verify that it was appropriate to include this early cruise in an analysis of Arctic Cod summer distribution patterns, a sensitivity analysis both including and excluding this cruise was conducted. The results of all analyses were virtually identical; therefore, T/S Oshoro-Maru IV 2008 was included in summer season analyses. Due to considerable differences in oceanographic and bathymetric conditions and due to their spatial separation, analyses were conducted separately for the Chukchi and Beaufort seas.

To describe Arctic Cod distribution patterns and the impact of environmental drivers on those patterns, two separate analyses were undertaken using GAM. The first analysis described the spatial distribution of Arctic Cod abundance using latitude and longitude as covariates. Environmental conditions were strongly confounded with spatial location; for example, in the Beaufort Sea depth increased with latitude as sampling moved both northerly and offshore. Thus, I modeled spatial patterns separately from assessing the effects of environmental covariates. Spatial and environmental analyses were conducted for each of the three length classes of Arctic Cod in the Chukchi and Beaufort seas. The spatial model was fit as follows:

(1) log*(count of Arctic Cod)* ~ *s(latitude, longitude)* + *log(area swept)*

where log denotes the natural logarithm and *s* denotes a smooth function of latitude and longitude estimated using a thin-plate regression spline. The second analysis investigated the impact of environmental correlates by modeling Arctic Cod abundance as a function of selected environmental covariates:

(2) log*(count of Arctic Cod)* ~ f_1*(depth)* + f_2*(temperature)* + f_3*(salinity)* + *log(area swept)*

where the f_i are smooth functions of the respective covariates estimated using thin-plate regression splines. For the environmental analysis, a model selection approach was used to select a best-fitting model. To evaluate the effect of each environmental covariate on Arctic Cod abundance, a suite of seven models was developed for each size class and in each sea, where every combination of environmental variables was considered. Within a size class and a sea, models were compared and the model with the lowest Akaike Information Criterion (AIC) was selected as the best performing model. Results from the best-fitting model for each size class were visually examined to describe the estimated relationships between Arctic Cod abundance and the environmental predictors. Arctic Cod abundance in different water masses could be identified when the best-performing environmental model included both temperature and salinity. Literature values characterizing typical water mass temperature and salinity ranges in the Chukchi Sea (Danielson et al. 2017) or Beaufort Sea (Norcross et al. 2018) were overlaid on relationships of Arctic Cod abundance relative to those variables to determine patterns of Arctic Cod abundance with respect to water mass.

Environmental model residuals suggested some degree of spatial autocorrelation among sites, where sites closer to each other were more similar than sites that were located farther apart. Both spatial and environmental models were tested for residual spatial autocorrelation by plotting the semivariance of model residuals as a function of distance between sampling points by year. Data for all length classes were combined to determine the spatial relationship between stations in each sea within a year. Comparison of AIC between the full model with spatial autocorrelation and the full model without spatial autocorrelation indicated slightly lower values (Chukchi Sea: ΔAIC = 2; Beaufort Sea: ΔAIC = 10) and thus a modest preference for the models that include a spatially autocorrelated error structure. Each environmental model, therefore, included an exponential decline in residual correlation with distance, as well as a nugget effect, conditioned on sampling year. Spatial correlation scale parameters (range and nugget) were estimated independently for each sea using the full model and included in all subsequent models. Due to statistical programming constraints caused by the inclusion of a spatially autocorrelated error structure, the dispersion parameter of the negative binomial distribution was estimated independently using the full model and fixed for each sea. After the incorporation of a spatially correlated error structure in the environmental model, both the spatial models and environmental models met assumptions of independence.

The completion of the spring cruise in the Chukchi Sea in June 2017 provided a seasonal comparison of offshore Arctic Cod abundances. As these data were collected in spring rather than summer, they were not included in the previously described spatial analysis. However, the spring abundance data were directly compared to abundance from a cruise conducted during summer 2017 in the southern Chukchi Sea. The two research efforts used the same gear and sampled from the Bering Strait (66.4 °N) to Cape Lisburne (69 °N). Due to small number of sample stations within the area of overlap (spring n = 8, summer n = 14), I was not able to develop a geostatistical model and instead compared abundance of Arctic Cod between spring and summer using a non-parametric (rank-based) Wilcoxon two-sample test. The test assumes that sampling in each season resulted in independent random samples that were representative of the area of overlap. Several August hauls caught large numbers of fish ≤70 mm, a size that was not observed in June. These small fish presumably consist of young-of-the year fish that were too small to be retained by the beam trawl in June. Therefore, instead of statistically comparing overall seasonal abundances for all sizes of Arctic Cod, I only applied to Wilcoxon two-sample test to compare seasonal abundances for fish >70 mm, i.e., those fish that were available to be caught by the gear in both spring and summer. Mean values of depth, temperature, and salinity for each season are reported; however, environmental data were not available for two stations sampled in August 2017.

Results

A total of 697 hauls from 21 cruises over 13 years were available for analysis (Table 1). The number of hauls conducted annually ranged from 5 to 88 in the Chukchi Sea and 18 to 97 in the Beaufort Sea. Sampling was primarily conducted in late summer during the ice-free season, but included samples from as early as 9 June to as late as 10 October in the Chukchi Sea and from 29 July to 4 September in the Beaufort Sea. Bottom water in the Chukchi Sea ranged from -1.8 to 10.9 °C, with salinities from 27.2 to 34.5 PSU. In comparison, conditions in the Beaufort Sea lacked the warmest and very coldest temperatures, with a range from -1.6 to 4.8 °C, and had salinities from 29.2 to 34.9 PSU.

When pooling data across all years, Arctic Cod showed latitudinal patterns in abundance in the Chukchi Sea and a strong longitudinal gradient in the Beaufort Sea. Generally, abundance of Arctic Cod in the Chukchi Sea showed a south to north gradient, with the highest abundance values north of Cape Lisburne (Figure 2). In the Beaufort Sea, Arctic Cod CPUE showed a predominantly west to east gradient, with the highest abundance west of 150 °W (Figure 2). Length frequencies of the catches were similar across both study regions; Arctic Cod ranged from 11 mm to 260 mm in the Chukchi Sea and from 21 mm to 230 mm in the Beaufort Sea (Figure 3). However, the modal length was 40 mm in the Chukchi Sea compared to 60 mm in the Beaufort Sea.

Spatial Analysis

In the Chukchi Sea, GAM analysis of trawl catches revealed distinct patterns of Arctic Cod distribution by size class. The small size class of Arctic Cod was most abundant in the northern Chukchi Sea, north of approximately 68 °N (Figure 4), where the Bering Chukchi Summer Water mass is commonly detected, while fewer small Arctic Cod were found south of 68 °N. The distribution of the medium size class was different when compared to the distribution of the small size class and did not show the same region of abundance in the NE Chukchi Sea. Medium-sized Arctic Cod were present across the entire Chukchi Sea shelf and showed pockets of high abundance in both nearshore and offshore regions. However, the regions of high abundance for the medium size class were not the same as the regions of high abundance for the small size class, offshore at 169 °W and north of 70 °N (Figure 4). Finally, the large size class of Arctic Cod was less abundant in the nearshore region and more abundant beginning ~80 km offshore and extending seaward, with an area of higher abundance south of Cape Lisburne (Figure 4). Deviance explained for the small, medium, and large size class models was 24.4%, 20.2%, and 57.5%, respectively (Table 2).

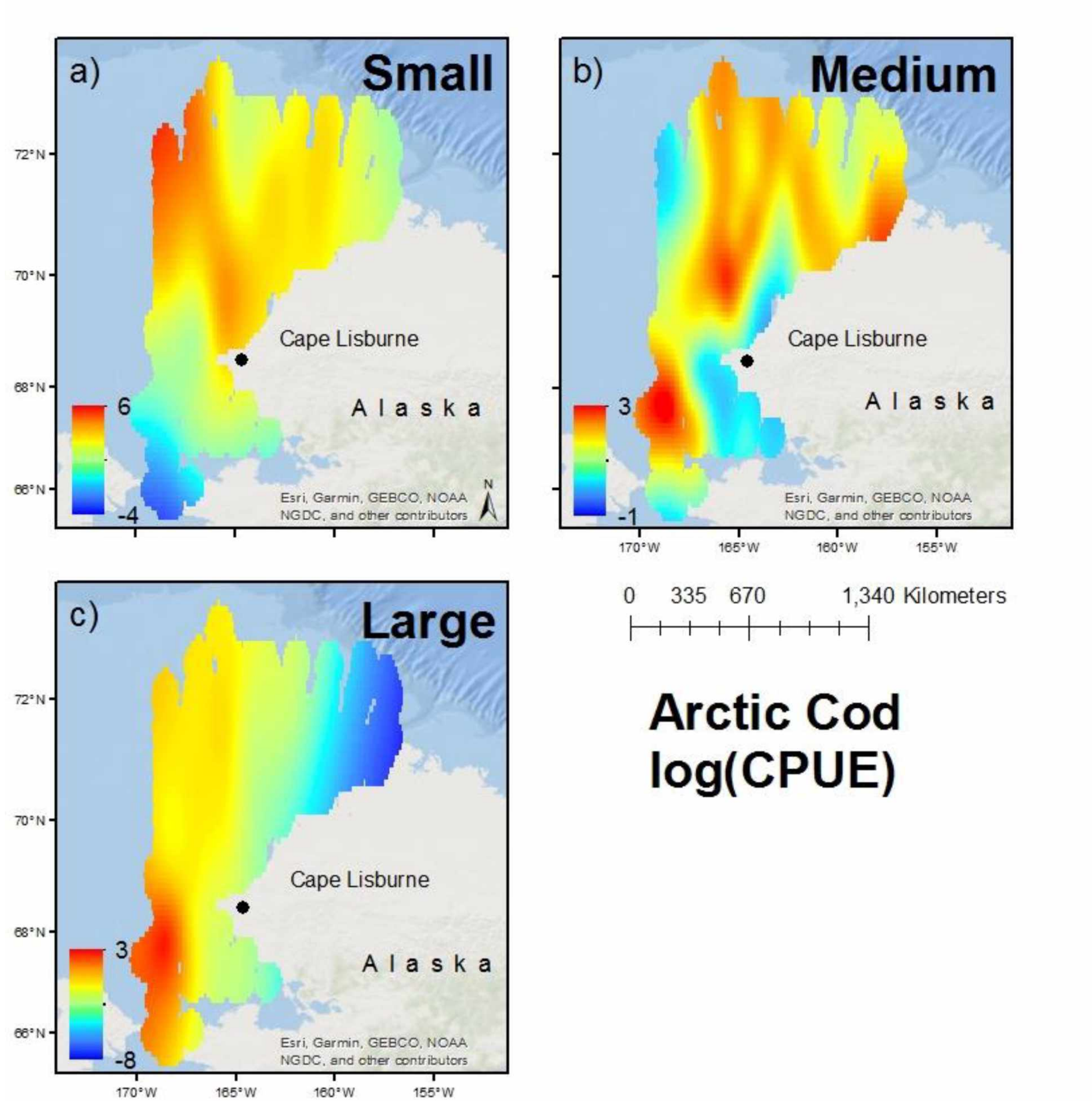

Figure 4. Spatial distribution of Arctic Cod catch per unit effort (CPUE, no. of fish per 1,000 m^2) in the Chukchi Sea for a) small ($\leq$70 mm), b) medium (71 – 130 mm), c) large (>130 mm) size classes. Abundances as predicted by generalized additive model (GAM) using a smooth function of latitude and longitude, shown on the log scale.

Table 2. Results of generalized additive models (GAM) for spatial distribution of Arctic Cod, latitude and longitude as explanatory variables (see Equation 1). Separate models developed in each sea and for each size class. θ parameter used for negative binomial parameterization, estimated degrees of freedom (edf), chi-square statistic, p-value denoting significance of latitude and longitude covariates, Akaike Information Criterion (AIC), and deviance explained.

Region	Size Class	θ	edf	chi-square	p-value	AIC	Deviance Explained
Chukchi	Small	0.19	19.5	99.3	<0.0001	1928.0	24.4%
Chukchi	Medium	0.40	26.6	67.0	<0.0001	1642.0	20.2%
Chukchi	Large	0.18	13.7	58.1	<0.0001	426.9	57.5%
Beaufort	Small	0.38	13.4	300.2	<0.0001	1073.2	62.7%
Beaufort	Medium	0.53	7.6	61.4	<0.0001	1051.0	22.9%
Beaufort	Large	0.19	3.0	23.1	<0.0001	353.9	21.7%

Similar to the Chukchi Sea, the GAM spatial analysis in the Beaufort Sea also found distinct, size-based patterns of Arctic Cod distribution. The small size class was distributed primarily along a west to east gradient, with an area of high abundance west of 150 °W, and another smaller area of abundance nearshore and east of 144 °W (Figure 5). There was also a nearshore to offshore gradient, where small Arctic Cod were distributed close to shore; however, the western aggregation was dispersed across the width of the entire Beaufort Sea shelf (to ~80 km), more than the eastern aggregation that was generally distributed closer to shore (within ~50 km). Abundance of the medium size class showed a less extreme longitudinal gradient than the small size class, and while abundance was highest west of 150 °W, medium Arctic Cod were diffuse across the entire Alaskan Beaufort Sea shelf. Unlike the small size class, medium-sized Arctic Cod did not show a separate area of high abundance east of 144 °W. The large size class of Arctic Cod was distributed offshore, beyond ~60 km. The deviance explained for the small, medium, and large size class analysis was 62.7%, 22.9%, and 21.7%, respectively (Table 2).

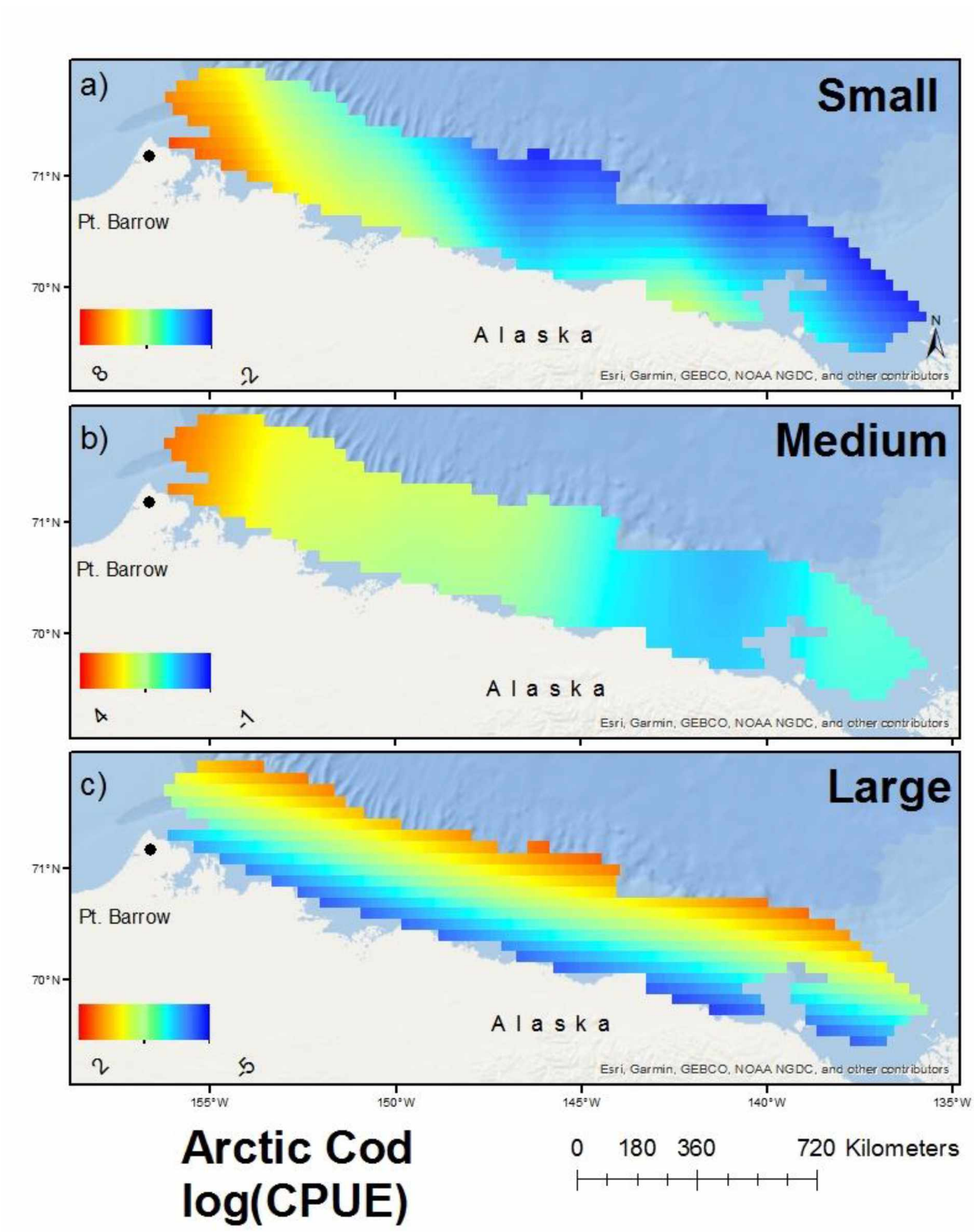

Figure 5. Spatial distribution of Arctic Cod catch per unit effort (CPUE, no. of fish per 1,000 m^2) in the Beaufort Sea for a) small ($\leq$70 mm), b) medium (71 – 130 mm), c) large (>130 mm) size classes. Abundances as predicted by generalized additive model (GAM) using a smooth function of latitude and longitude, shown on log scale.

Environmental analysis

In the Chukchi Sea, the influence of the environmental variables on Arctic Cod abundance depended on size class. For the small size class of Arctic Cod, the top performing model included both temperature and salinity (Table 3). A dome-shaped curve described the relationship between Arctic Cod abundance and temperature with a peak at 4–5 °C, while abundances increased linearly with salinity to a maximum of 34.5 PSU (Figure 6). For Arctic Cod in the medium size class, the top performing model only included depth and abundance increased linearly with depth (Table 3, Figure 6). The best-fitting model for the large size class of Arctic Cod in the Chukchi Sea also only included depth as a covariate; there was a positive relationship between depth and abundance of large Arctic Cod in the Chukchi Sea (Table 3, Figure 6).

As in the Chukchi Sea, the relationships between environmental variables and abundance of Arctic Cod in the Beaufort Sea were specific to size classes. The best-fitting model for the small size class in the Beaufort Sea included both temperature and salinity (Table 4). Abundance of small Arctic Cod in the Beaufort Sea increased linearly to a maximum temperature of 4.8 °C, which was similar to the Chukchi Sea, and was highest at intermediate salinities; small Arctic Cod were less abundant at the lowest (<31 PSU) and highest (>34 PSU) salinity (Figure 7). The top-performing model for the medium size class in the Beaufort Sea included both depth and temperature (Table 4), unlike the analogous model in the Chukchi Sea, which only included depth. In the Beaufort Sea, abundance of medium Arctic Cod increased with depth to approximately 200 m and then began to decline; medium Arctic Cod abundance increased linearly with temperature (Figure 7). As in the Chukchi Sea, the top performing model for the large size class included only depth as a covariate (Table 4). Notably, large Arctic Cod abundance increased with depth in the Beaufort Sea to about 400 m, but as depth surpassed 400 m, abundance of Arctic Cod decreased (Figure 7). The shape of the relationship between depth and abundance was similar for both medium and large Arctic Cod, but the medium size class was more abundant at shallow depths than the large size class of Arctic Cod.

Table 3. Results of generalized additive models (GAM) in the Chukchi Sea for environmental covariates, depth, temperature, and salinity (see Equation 2). Suite of models developed for each size class, + denotes variables included in each model. The following statistics are reported: -log(likelihood), AIC, ΔAIC. Model performance ranked from best (1) to worst (7) using ΔAIC. ΔAIC calculated as the difference from the lowest AIC value for a size class and sea. θ parameter estimated independently and fixed, θ = 0.345.

Size Class	s(Depth) *(13–90 m)*	s(Bottom Temperature) *(-1.8–10.9 °C)*	s(Bottom Salinity) *(27.2–34.5 PSU)*	-(logLikelihood)	AIC	ΔAIC	Model Rank
Small		+	+	-1011.1	2034.1	0.0	1
	+	+	+	-1014.2	2044.3	10.2	2
		+		-1032.7	2073.5	39.3	3
	+	+		-1054.5	2121.1	86.9	4
			+	-1075.7	2159.5	125.4	5
	+		+	-1081.5	2174.9	140.8	6
	+			-1115.9	2239.8	205.7	7
Medium	+			-908.0	1824.0	0.0	1
			+	-919.7	1847.3	23.4	2
	+		+	-919.7	1851.3	27.3	3
		+	+	-920.6	1853.1	29.1	4
	+	+	+	-920.2	1856.5	32.5	5
	+	+		-927.8	1867.6	43.6	6
		+		-933.0	1874.0	50.0	7
Large	+			-1224.2	2456.4	0.0	1
	+	+		-1223.7	2459.5	3.1	2
	+		+	-1247.0	2506.0	49.6	3
	+	+	+	-1312.7	2641.4	185.0	4
			+	-1477.5	2962.9	506.5	5
		+	+	-1574.3	3160.6	704.2	6
		+		-1595.1	3198.2	741.8	7

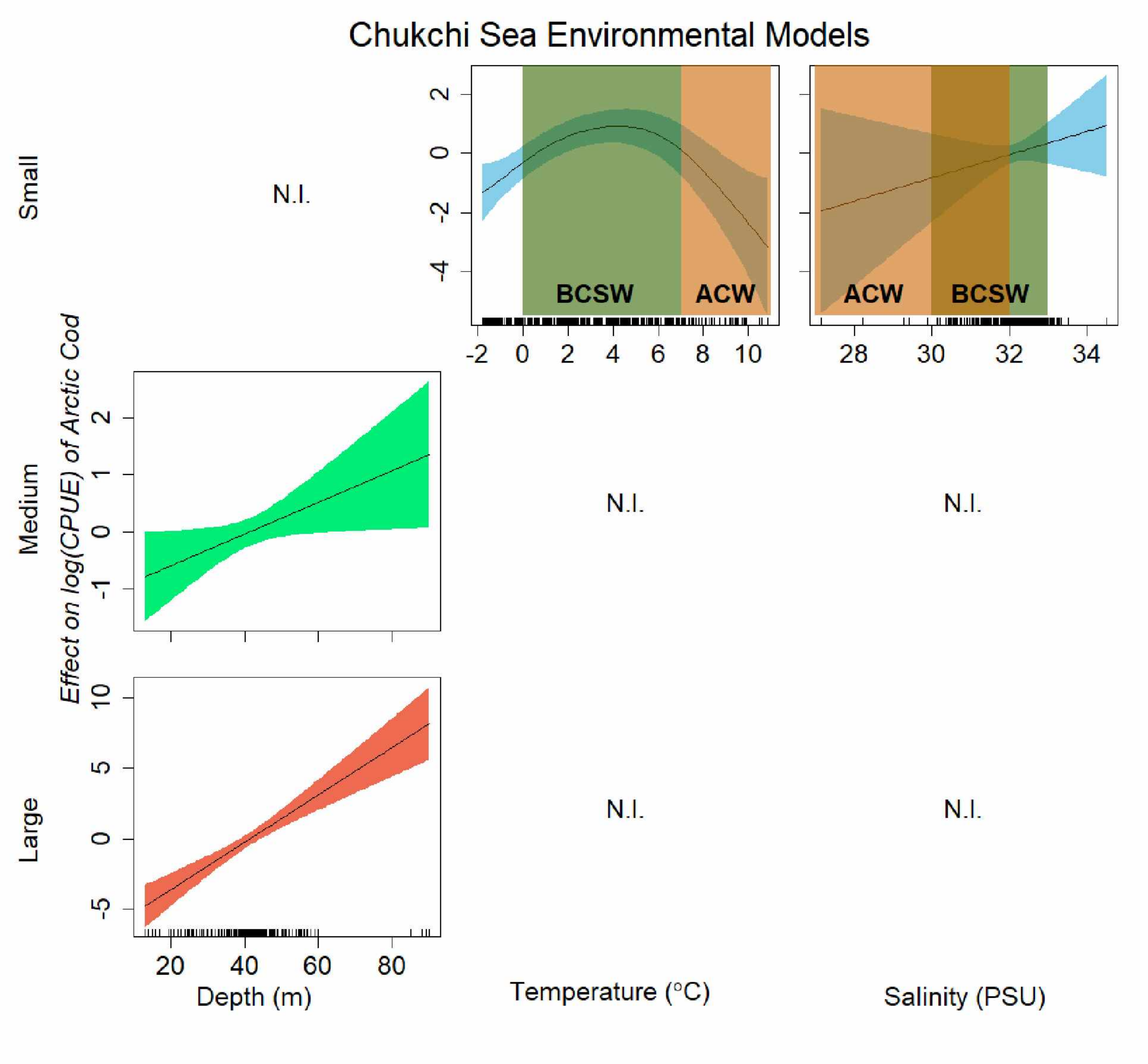

Figure 6. Estimated effects of three environmental variables on log(CPUE) of three size classes of Arctic Cod in the Chukchi Sea based on generalized additive model (GAM) analysis. Y-axis is magnitude of effect, rug along x-axis marks data values, colored envelopes are 95% confidence intervals. Results from the best model (Table 3) are displayed, variables excluded from the best model marked with N.I. (not included). Temperature and salinity measured at the seafloor. Characteristic water mass temperature and salinity values overlaid (BCSW = Bering Chukchi Summer Water, ACW = Alaska Coastal Water).

Table 4. Results of generalized additive models (GAM) in the Beaufort Sea for environmental covariates, depth, temperature, and salinity (see Equation 2). Suite of models developed for each size class, + denotes variables included in each model. The following statistics are reported: -log(likelihood), AIC, ΔAIC. Model performance ranked from best (1) to worst (7) using ΔAIC. ΔAIC calculated as the difference from the lowest AIC value for a size class and sea. θ parameter estimated independently and fixed, θ = 0.878.

Size Class	s(Depth) *(9–987 m)*	s(Bottom Temperature) *(-1.6–4.8 °C)*	s(Bottom Salinity) *(29.2–34.9 PSU)*	-(logLikelihood)	AIC	ΔAIC	Model Rank
Small		+	+	-620.5	1252.9	0.0	1
	+	+	+	-594.8	1257.2	4.3	2
	+	+		-700.6	1413.1	160.2	3
	+		+	-754.5	1521.0	268.1	4
			+	-756.7	1521.3	268.4	5
		+		-767.4	1542.8	289.8	6
	+			-780.7	1569.5	316.6	7
Medium	+	+		-501.4	1014.7	0.0	1
	+	+	+	-503.0	1022.0	7.3	2
		+		-543.7	1095.5	80.7	3
		+	+	-552.3	1116.6	101.8	4
	+			-620.7	1249.3	234.6	5
			+	-629.8	1267.6	252.9	6
	+		+	-633.1	1278.2	263.5	7
Large	+			-721.4	1450.9	0.0	1
	+	+		-724.0	1460.0	9.1	2
		+		-740.2	1488.4	37.5	3
	+		+	-764.1	1540.3	89.4	4
			+	-767.8	1543.6	92.7	5
	+	+	+	-766.8	1549.5	98.6	6
		+	+	-775.7	1563.4	112.5	7

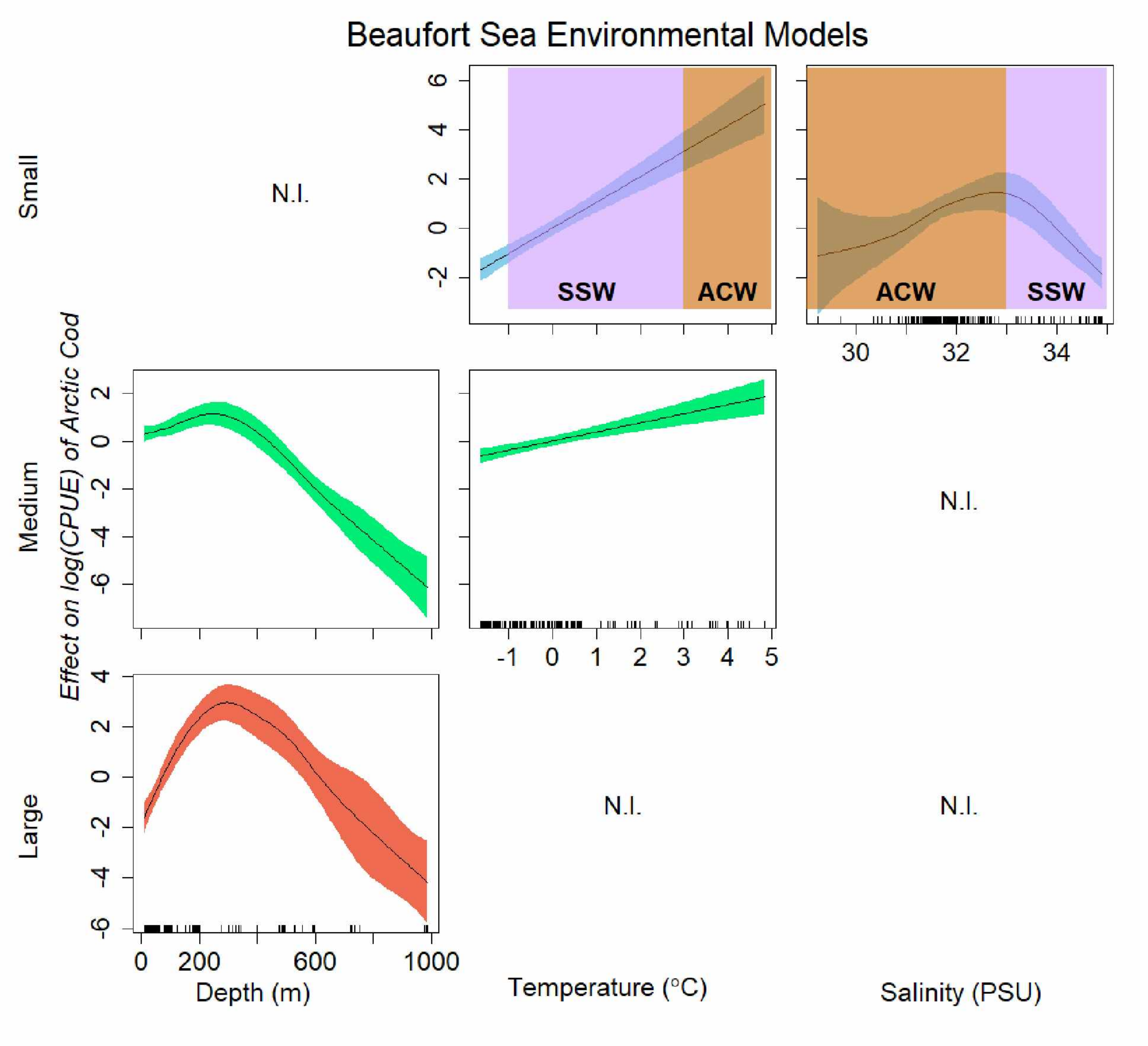

Figure 7. Estimated effects of three environmental variables on log(CPUE) of three size classes of Arctic Cod in the Beaufort Sea based on generalized additive model (GAM) analysis. Y-axis is magnitude of effect, rug along x-axis mark location of data values, colored envelopes are 95% confidence intervals. Results from the best model (Table 4) are displayed, variables excluded from the best model marked with N.I. (not included). Temperature and salinity measured at the seafloor. Characteristic water mass temperature and salinity values overlaid (SSW = Summer Shelf Water, ACW = Alaska Coastal Water).

Seasonal analysis

Comparison of Arctic Cod catches between spring and summer in the southern Chukchi Sea revealed striking differences in fish abundance. Overall mean abundance of Arctic Cod was much lower in June 2017 compared to August 2017 (Table 5). During the spring, Arctic Cod was scarce; only four individuals were captured at three sampling locations (Figure 8). In contrast, Arctic Cod CPUE was higher at locations sampled in August 2017 (Table 5). There were summer hauls that captured high abundances of small-sized Arctic Cod, including one station with a CPUE of 832 fish per 1,000 m^2, with individuals ranging from 31 to 70 mm in length. Catch length-frequency composition in the summer contrasts with the Arctic Cod caught in the spring, where only one fish <70 mm was captured (Figure 8). Arctic Cod 31 to 70 mm captured in August were likely young-of-the-year; these small fish were not available to the beam trawl in June due to both their pelagic distribution and small size before the summer growing season. Therefore, to verify that the observed seasonal differences in CPUE were truly differences in abundance, and not the result of small fish growing in size and descending to the seafloor to become increasingly represented in the catch as the summer progressed, only spring and summer CPUE of individuals >70 mm were statistically compared. Seasonal differences in CPUE were significant after the exclusion of small, highly abundant Arctic Cod in August (Table 5, Wilcoxon two-sample test, $p = 0.03$).

Table 5. Arctic Cod mean CPUE in spring and summer 2017 in the southern Chukchi Sea. Mean and (standard deviation) environmental conditions reported for depth (m), temperature (°C), salinity (PSU). Mean and (standard deviation) CPUE reported for all Arctic Cod as well as only Arctic Cod >70 mm. CPUE significantly different ($p<0.05$) between spring and summer for Arctic Cod >70mm.

Season	Station (n)	Depth	Temperature	Salinity	Size class	CPUE
Spring	8	42.4(10)	1.59(1.27)	32.39(0.40)	All	0.80(1.16)
					>70 mm	0.60(1.09)
Summer	14	39.1(13)	4.18(0.95)	32.26(0.56)	All	70.31(219.92)
					>70 mm	3.02(3.52)

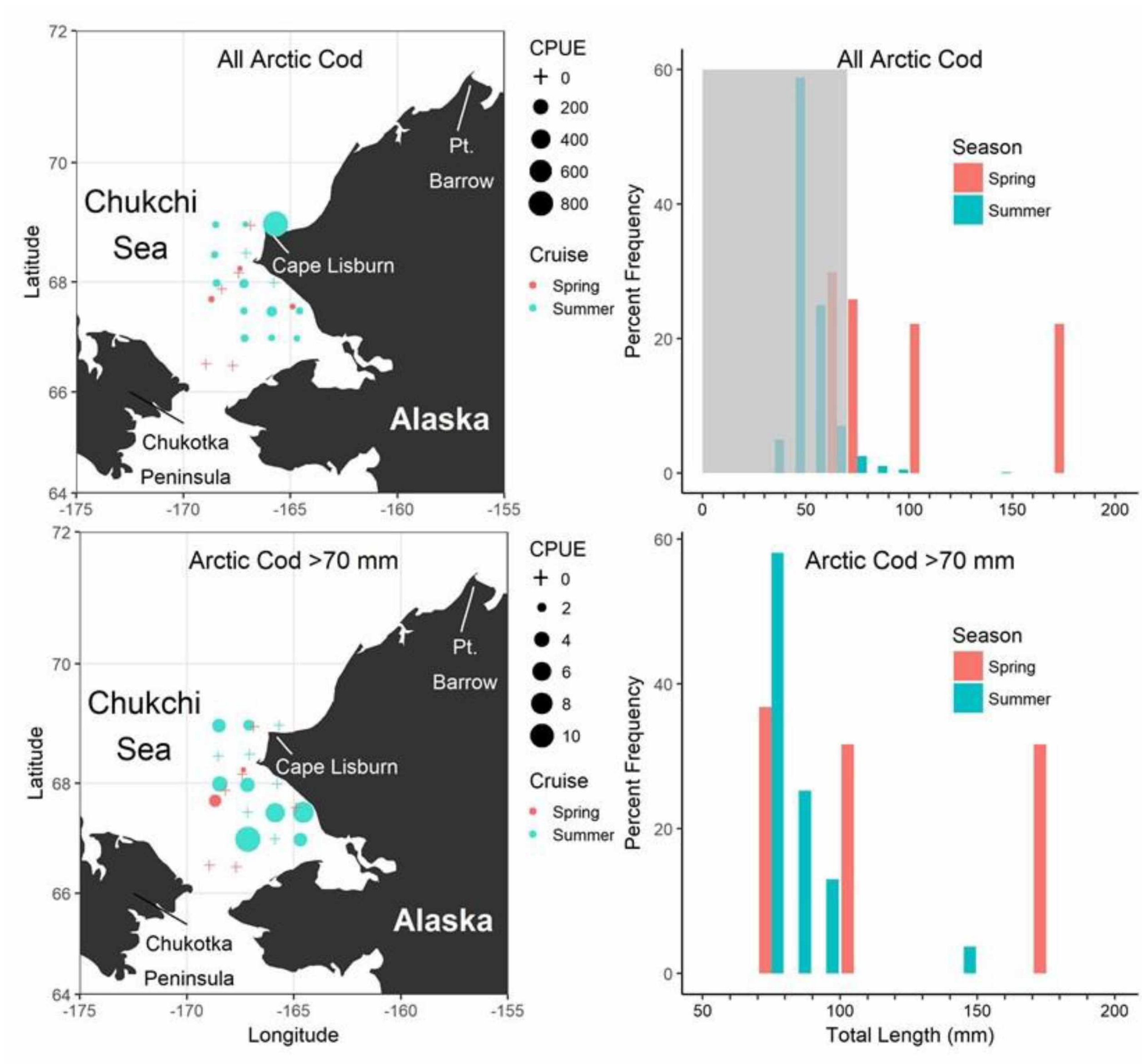

Figure 8. Distribution and length frequency of Arctic Cod in the Chukchi Sea in spring and summer 2017. Length frequency scaled by CPUE. Top two panels are all captured sizes of Arctic Cod, total CPUE (fish per 1,000 m^2) spring = 6.43, summer = 984.40. Bottom two panels are only Arctic Cod >70 mm, total CPUE spring = 4.51, summer = 42.29; gray box in top right shows small fish excluded from lower two plots. Note difference in scale between top left and bottom left plot.

Discussion

By visualizing the distribution patterns of small, medium, and large Arctic Cod, understanding of ontogenetic shifts in distribution as well as possible migration patterns of this species in the Pacific Arctic has been improved. Furthermore, by relating patterns in distribution to environmental variables, I provide insight into potential mechanisms driving Arctic Cod distribution. The importance of environmental covariates varies with to each of the three size classes and suggest that the relative influence of external drivers on Arctic Cod distribution influences life stages differently. A comparison of abundance between spring and summer in the southern Chukchi Sea revealed seasonal differences in Arctic Cod abundance. Finally, I hypothesize that both ontogenetic and seasonal movements of Arctic Cod described in this study are evidence of a migration scenario that may be used to explain Arctic Cod movement patterns in the Pacific Arctic.

There are several assumptions implicit in this analysis that could impact my interpretation of Arctic Cod distribution patterns and potential environmental drivers of those patterns. First, I assume that catches of Arctic Cod are representative of its abundance in the demersal environment. The current study used one gear type and sampled over a large geographic extent, both of which reduce bias when interpreting CPUE as a representative measure of population biomass (Maunder et al. 2006). Second, I assume that our sampling gear is reasonably effective at capturing all size classes of available Arctic Cod. The 4 mm mesh codend liner ensures that this is an accurate assumption for individuals <150 mm; however, a gear selectivity study indicates that the PSBT may not be the most effective sampling gear for Arctic Cod >150 mm (Kotwicki et al. 2017). Despite this selectivity, the results presented here nevertheless capture the bulk of the Arctic Cod length distribution, as similar studies deploying a net with higher selectivity for large fish found that the majority of Arctic Cod catch was <150 mm in both the Chukchi Sea (Goddard et al. 2016) and the Beaufort Sea (Rand and Logerwell 2010). Third, I assume that the negative binomial distribution is effective at accommodating both the non-normal distribution of abundance and the high proportion of zero catches in the data. Sensitivity analysis comparing the performance of other distribution families (i.e., normal distribution with log-transformed response and tweedie distribution) showed that the top performing model used a negative binomial distribution. Nevertheless, interpretation of analyses for the large size class should be undertaken cautiously, as there is a high proportion of zero-catch hauls for large fish. Finally, by pooling data across years, I assume that the spatial patterns in average fish abundance are not biased by interannual variability in catches. The inclusion of sampling year as a random effect in the model was considered, but ultimately omitted, as spatial patterns were confounded by variable sampling designs among years and cruises.

Spatial Analysis

In the Chukchi Sea, visualizing the distribution of the small size class of Arctic Cod suggests oceanic transport of the juvenile life stage of this species. Due to small body size and weak swimming ability, the distribution of small individuals, such as the ≤70 mm Arctic Cod considered here, is largely influenced by the direction and speed of the prevailing oceanic currents (Graham and Hop 1995). Because age-0 Arctic Cod descend in the water column throughout their first summer (Geoffroy et al. 2016), the small Arctic Cod captured in the demersal trawl had likely descended to the seafloor recently, after being subjected to movement by pelagic ocean currents. In addition to demersal surveys, pelagic acoustic surveys in the Chukchi Sea have also detected large numbers of small, 30–40 mm, age-0 Arctic Cod in the water column in the northern Chukchi Sea (De Robertis et al. 2017a; De Robertis et al. 2017b). Because Arctic Cod this size are predominantly age-0 (Helser et al. 2017), the distribution of small individuals in the late summer likely reflects the transport of young-of-the-year Arctic Cod hatched in the spring (Bouchard and Fortier 2011) and advected from hatch locations via ocean currents. Detection of pelagic age-0 Arctic Cod (De Robertis et al. 2017b) as well as demersal environment is evidence that small Arctic Cod may be transported with moving water masses.

The primarily northward flow of water through the Bering Strait and across the Chukchi Sea (Weingartner et al. 2013) suggests that the abundance of age-0 Arctic Cod found in the northeast Chukchi Sea in the late summer could have been transported from spawning locations in the southern Chukchi and northern Bering seas in Bering Shelf Water (BSW) and Anadyr Water (AW). Generally, Arctic Cod hatch from buoyant eggs, occupy the water column as larvae, and descend to a demersal environment as they grow (Graham and Hop 1995; Ponomarenko 2000). Though still an area of active research, potential spawning grounds for Arctic Cod in the Pacific Arctic have been proposed near St. Lawrence Island and east of the Chukotka peninsula in the Pacific

Arctic (C. Vestfals, personal communication), and could be the source of age-0 Arctic Cod transported northward and captured in the northeast Chukchi Sea in late summer. However, the detection of larvae throughout the Canadian Arctic (Bouchard and Fortier 2011) indicates that spawning grounds in the Bering and Chukchi seas may be only a few of several spawning regions throughout the Pacific range of Arctic Cod.

As a result of the orientation of the Alaskan coastline, the distribution patterns in the Beaufort Sea of small Arctic Cod display a primarily west to east gradient, coupled secondarily with an inshore to offshore gradient. As in the Chukchi Sea, however, the distribution of small individuals in the Beaufort Sea is likely largely influenced by oceanic currents. A component of the Alaska Coastal Current (ACC), which may play a role in transporting Arctic Cod northward in the Chukchi Sea, continues to flow along the Alaskan Coast, around Pt. Barrow, and into the Beaufort Sea (Okkonen et al. 2009). Barrow Canyon in the northern Chukchi Sea facilitates the movement of the ACC towards the Beaufort Sea (Pickart et al. 2005) and could effectively transport larval Arctic Cod into the western Beaufort Sea as it does for zooplankton and other small particles (Ashjian et al. 2005; Berline et al. 2008). This is corroborated by a 2008 demersal trawl survey conducted near Pt. Barrow that found the highest abundance of Arctic Cod near the head of Barrow Canyon and was associated with water of Chukchi Sea origin traveling east along the shelf break (Logerwell et al. 2011). Further, small fish were also detected in the ACC in a plume extending 300 km eastward of Barrow Canyon (Crawford et al. 2012), demonstrating that small Arctic Cod may be transported into the Beaufort Sea via eastward flowing currents.

Eastern and western aggregations of small Arctic Cod in the Beaufort Sea, separated by a gap from 150 °W to 144 °W, suggests two distinct populations. Despite the prevailing eastward flow of water, the spatial separation indicates that Arctic Cod in the eastern Beaufort Sea did not originate in the Chukchi Sea. Larval, juvenile, and adult Arctic Cod are commonly captured in the Canadian Beaufort Sea (Bouchard and Fortier 2011; Geoffroy et al. 2011; Walkusz et al. 2013) and could be a source of small Arctic Cod in the eastern US Beaufort Sea. In 2011, pelagic, larval Arctic Cod were most abundant in the eastern US Beaufort Sea when compared to the western US Beaufort Sea (Gallaway et al. 2017), suggesting that some Arctic Cod in the US Beaufort Sea originate from Canadian sources. The low abundance of small Arctic Cod between 150 °W and 144 °W is not an artifact of sparse sampling effort in the middle section, as the station sampling density is similar across the entire Beaufort Sea shelf; nor is it the result of a single year of low Arctic Cod abundance, as this region was sampled over multiple years. The distribution patterns are corroborated by a population genetic study in the Pacific Arctic. While Arctic Cod comprises a single population, a significant difference in microsatellite alleles between Arctic Cod from the southern Chukchi Sea and the central Beaufort Sea implies some degree of spatial genetic differentiation consistent with an isolation-by-distance pattern (Wilson et al. 2017; Wilson et al. 2019). Together, spatial and genetic information indicate that small Arctic Cod across the Beaufort Sea shelf could belong to two spatially segregated groups from different spawning locations.

In both the Chukchi and Beaufort seas, distribution patterns of small and medium Arctic Cod suggest that the medium size class actively disperses from areas occupied by the smallest fish. The small size class had a region of high abundance in the northeast Chukchi Sea that was not seen in the medium size class. As fish develop, swimming ability improves (Webb 1994) and juveniles may disperse from nursery grounds to adult habitats (Gillanders et al. 2003). Improved dispersal capabilities gained with increasing body size could explain the spread of the medium size class beyond the confines of the areas occupied by small Arctic Cod in the Chukchi and Beaufort seas. Animals are often distributed with respect to resource availability to maximize fitness and reduce competition (Fretwell and Lucas 1969). The northeast Chukchi Sea and western Beaufort Sea, where there were regions of high abundance of the medium size class, are areas of high summer production (Walsh et al. 2005; Sigler et al. 2011). Therefore, mid-sized individuals may be maximizing growth by dispersing to productive feeding grounds. Many medium Arctic Cod individuals in the 71–130 mm size range are age-1, though given the overlap in age-at-length for Arctic Cod, the medium size class likely contains a mixture of age-1 and age-2 fish (Craig et al. 1982; Helser et al. 2017; Norcross et al. 2017). Age-1 Arctic Cod are generally not yet sexually mature (Craig et al. 1982; Kent et al. 2016), though some individuals in the Atlantic Arctic in Svalbard reach maturity at age-1 (Nahrgang et al. 2016). Thus, the northeast Chukchi Sea and west Beaufort Sea may act as feeding grounds for sexually immature Arctic Cod.

The large size class of Arctic Cod showed evidence of offshore ontogenetic movement in both the Chukchi and Beaufort seas. The wide and shallow Chukchi Sea does not have the rapid increase in depth of the Beaufort Sea, which has a narrow shelf and steep slope, and yet in both cases, large Arctic Cod was more abundant offshore, beginning around 80 km in the Chukchi Sea and 60 km in the Beaufort Sea and extending seaward (Figures 4, 5). High offshore abundance of large Arctic Cod is distinct from the nearshore patterns of smaller size classes, and indicates that larger Arctic Cod tend to move offshore. That is consistent with smaller Arctic Cod in nearshore shallow water (40–100 m) and larger fish offshore at depths >100 m (Frost and Lowry 1983; Rand and Logerwell 2010). Though Arctic Cod is a small bodied species, adults >182 mm in length are nevertheless capable of migrating at least 192 km in the Atlantic Arctic (Kessel et al. 2017). In the current study, a linear estimate from the shore to the center of large Arctic Cod abundance is 80–200 km, depending on the sea and position along the coast (Figures 4, 5). Compared to migratory capacities of Arctic Cod in the Atlantic Arctic (Ponomarenko 1968; Kessel et al. 2017), a migration distance of 80–200 km from nearshore to offshore in the Pacific Arctic is plausible.

Offshore movement of large Arctic Cod may be a component of adult spawning migrations and may also reduce the likelihood of cannibalism on smaller conspecifics. In the Chukchi Sea, several spawning grounds have been proposed in the northern Bering Sea and near the Chukotka peninsula (C. Vestfals, personal communication). The abundance of the large size class of Arctic Cod, both offshore and south of Cape Lisburne in the late summer, could reflect a movement towards these southern winter spawning locations. Additionally, spatial segregation of size classes could be advantageous by reducing the possibility of predation of large fish on smaller conspecifics. While cannibalism is uncommon for Arctic Cod as they are primarily planktivorous and rarely are encountered with fish in their gut contents (Rand et al. 2013; Gray et al. 2016), it has known to occur (Benoit et al. 2010). The low occurrence of cannibalism in Arctic Cod may be precisely because small and large fish are spatially segregated and cannibalistic opportunities are scarce. Similarly, small and large Arctic Cod are vertically segregated in the water column (Geoffroy et al. 2016), suggesting that segregation of size classes, whether vertical or horizontal, reduces opportunities for cannibalism. Walleye Pollock, a closely related gadid species in the Pacific, is highly cannibalistic where the distributions of small and large fish overlap in the Bering Sea (Wespestad 2000; Mueter et al. 2006) but less so when distributions are segregated in the Gulf of Alaska (Hollowed et al. 2000). Therefore, offshore distribution of Arctic Cod may be explained by adults spawning migrations, and may also be beneficial by reducing predation levels on smaller conspecifics.

Environmental Analysis

Relating environmental variables to Arctic Cod abundance provides context for catches and suggests underlying mechanisms to explain observed distribution patterns. Generally, both availability of food resources and temperature influence habitat selection of ectothermic species (Crowder and Magnuson 1983). Food resources are distributed unevenly among water masses (Eisner et al. 2013; Danielson et al. 2017; Pinchuk and Eisner 2017; Smoot and Hopcroft 2017), which are identified by characteristic temperature and salinity ranges in the Chukchi and Beaufort seas. In addition, temperature has a direct physiological effect on growth rates of juvenile Arctic

Cod (Laurel et al. 2017) and likely influences their distribution. Depth also commonly influences distribution patterns and is associated with offshore migrations of other species such as Pacific Cod and Pacific Halibut (*Hippoglossus stenolepis*), in the neighboring Bering Sea (Shimada and Kimura 1994; Webster et al. 2013). In Alaskan waters, the addition of environmental information to species distribution maps has been identified as a recent research objective in the Alaska Essential Fish Habitat Research Plan, which is mandated by the Magnuson-Stevens Fishery Conservation and Management Act (Sigler et al. 2017). Characterizing the role of environmental conditions for Arctic Cod at different life stages moves towards this goal and identifies underlying processes influencing spatial patterns in distribution.

In the Chukchi Sea, small Arctic Cod were associated with the intermediate temperature and salinity of the highly productive Bering Chukchi Summer Water (BCSW) mass. BCSW is a commonly detected water mass throughout the northeast Chukchi Sea during the open water season, with temperatures ranging from 0 to 7 °C and salinity from 30 to 33.5 PSU (Danielson et al. 2017), which were the temperature and salinity ranges most commonly occupied by small Arctic Cod (Figure 6). Other water masses in the Chukchi Sea include the cooler Bering Chukchi Winter Water (BCWW) with temperatures from -2 to 0 °C and salinity from 30 to 33 PSU, and the warmer Alaska Coastal Water (ACW) with temperatures from 7 to 12 °C and salinity from 27 to 32 PSU (Danielson et al. 2017); however, small Arctic Cod were less abundant in these water masses. The distribution of small Arctic Cod predicted by the spatial analysis agrees with the results of the environmental analysis and predicts high abundances of small

Arctic Cod at locations where BCSW is frequently detected on the Chukchi Sea shelf. BCSW is a nutrient rich water mass with a characteristic zooplankton community of calanoid copepods and euphausiids (Eisner et al. 2013), which are prey for Arctic Cod (Rand et al. 2013; Gray et al. 2016). In contrast, the BCWW and ACW are less nutrient rich, and have smaller-bodied zooplankton communities, including species such as *Oithona similis*, *Calanus abdominalis*, and *Pseudocalanus* spp. (Eisner et al. 2013), which are marginal resources when compared to lipid-rich calanoid copepods (Falk-Petersen et al. 2009). Maximizing energy intake as a result of consuming high-quality prey resources is beneficial to Arctic Cod and results in increased growth rates and improved body condition (Hop et al. 1997). Therefore, distribution patterns of small Arctic Cod in the Chukchi Sea are likely influenced by the abundance and composition of prey resources in different water masses.

Though growth of Arctic Cod is temperature dependent, small Arctic Cod in the Chukchi Sea were not always most abundant at water temperatures that maximized growth, illustrating that resource availability is more influential than water temperature on Arctic Cod distribution. The highest abundance of the small size class of Arctic Cod in the Chukchi Sea was detected at 4–5 °C, while a lab-based temperature-dependent growth model estimated a much higher 9 °C thermal growth optimum for 45–70 mm Arctic Cod (Laurel et al. 2017). Water temperatures that would support optimum growth rates of small Arctic Cod are present in the Chukchi Sea, but the low abundance of Arctic Cod in those waters implies that occupying those waters is also costly. Small Arctic Cod may incur a cost of a sub-optimal temperature-dependent metabolic growth rate in exchange for the benefit of plentiful food resources in the BCSW; a trade-off that is common in fish-specific foraging theory (Crowder and Magnuson 1983). By comparison, in the Beaufort Sea, where the available temperatures were below thermal growth optima, it appears that occupying the warmest available water, despite potentially poor resource availability, may be the most advantageous strategy for growth.

In the Beaufort Sea, small Arctic Cod were primarily associated with relatively warm and moderately fresh water found near the Alaskan coast. Environmental conditions in the Beaufort Sea are markedly different from those found in the Chukchi Sea; the warmest sampled Beaufort Sea temperature of 5 °C is comparable to the intermediate temperatures found in the Chukchi Sea. Yet in both the Chukchi and Beaufort seas (Figures 6, 7), small Arctic Cod were most abundant in water temperatures 4–5 °C. However, the relationship between small Arctic Cod abundance and salinity differed between the Chukchi and Beaufort seas. Unlike in the Chukchi Sea where abundance increased linearly with salinity to a maximum of 34.5 PSU, small Arctic Cod in the Beaufort Sea were less abundant at salinities >34 PSU. Cold and saline water is associated with Summer Shelf Water (SSW), and suggest that the differing effect of salinity between seas is likely due to this association of small Arctic Cod with distinct water masses, characterized by a signature combination of temperature and salinity (Danielson et al. 2017).

The warm and fresh water occupied by small Arctic Cod in the Beaufort Sea is associated with nearshore coastal habitats and the eastward flowing ACW, freshened by input from rivers and coastal runoff (Okkonen et al. 2009; Carmack et al. 2015). This warm coastal water is not nutrient rich (Dunton et al. 2005), but does provide a thermal habitat that is advantageous for Arctic Cod. Though Arctic Cod is a cold-adapted species and capable of surviving in sub-zero temperatures (Osuga and Feeney 1978), it is more commonly found at temperatures above 0 °C (Crawford et al. 2012). Small Arctic Cod in the Beaufort Sea appear to be occupying the warmest available water to maximize growth. Higher growth rates afford several key advantages for the small size class of individuals, which is principally composed of age-0 fish (Helser et al. 2017). In harsh Arctic winters, survivorship increases dramatically when pre-winter size and body condition are good (Fortier et al. 2006; Heintz and Vollenweider 2010). In addition, as individuals grow larger, gape sizes and swimming speeds increase, enabling them to exploit a greater number of resources; as well, predation risk declines as larger fish become capable of evading predators (Scharf et al. 2000; Houde 2008). In the Beaufort Sea, the thermal advantages of warm, coastal water appear to be correlated with patterns of distribution of small Arctic Cod. Though the thermal advantages of warm coastal water may outweigh the costs of low nutrients and low production, this tradeoff could have negative energetic consequences for Arctic Cod growth and survival in the Beaufort Sea.

The positive relationship between depth and abundance (Figures 6, 7) indicates that depth is a key environmental component correlated with the offshore shift in distribution of the medium and large size classes of Arctic Cod in the Chukchi and Beaufort seas. In the Chukchi Sea, where sampled depths were 13–90 m, the increasing linear relationship with depth suggests that Arctic Cod moves to offshore, somewhat deeper locations as they grow larger. In the Beaufort Sea, where sampled depths reached nearly 1,000 m, medium and large Arctic Cod were most abundant to 200 and 400 m, respectively, demonstrating that as individuals increase in size, they move offshore to a specific bottom depth range. A nearly identical pattern was identified in the Canadian Beaufort, where larger fish (~90+ mm) were encountered at deep, offshore stations and the highest abundances of those fish were found at depths between 350–500 m (Geoffroy et al. 2011; Benoit et al. 2014; Majewski et al. 2016). The distribution pattern of Arctic Cod was attributed to distinctly layered water masses in the Canadian Beaufort Sea (Pickart 2004), with Arctic Cod occupying a layer of Atlantic Water, which was warmer than 0 °C and detected from 350–500 m depth. In the present study area, Atlantic Water was observed in the US Beaufort Sea at depths >250 m (Smoot and Hopcroft 2017; Norcross et al. 2018), and this was where large Arctic Cod were most abundant (Figure 7). Therefore, Arctic Cod occupies the Atlantic Water mass in both the US and Canadian Beaufort Sea. The impact of environmental variables on Arctic Cod abundance differed across the small, medium, and large size classes, which indicates that the environmental requirements or preferences of Arctic Cod change throughout its life cycle, and may drive differences in spatial distribution patterns in the Chukchi and Beaufort seas.

Seasonal Analysis

Springtime abundance of Arctic Cod in the southern Chukchi Sea was strikingly low compared to late summer abundance. Low springtime abundance of demersal Arctic

Cod during 2017, when only four fish were captured, was corroborated the following year when a June 2018 research cruise captured only two Arctic Cod at the same sampling locations (Danielson et al. 2018). While adult Arctic Cod were not present in the demersal environment in the southern Chukchi Sea in the spring. Small Arctic Cod (<20 mm) were captured in Bongo nets (R. Hopcroft, personal communication) concurrently sampled with the bottom trawl in June 2017 and 2018. Northward flowing currents and weak swimming abilities of small Arctic Cod suggests that these smallest fish were advected from more southerly waters into the southern Chukchi Sea study area. The bottom trawl gear used in June 2017 and 2018 was identical to the gear used in the late summer collections, that successfully captured demersal Arctic Cod in the same region. Though there were approximately half the number of stations sampled in June when compared to August, the stations were distributed across the study area to maximize spatial sampling extent (Figure 8); therefore, the collections during the spring season likely truly represent a lower abundance of adult Arctic Cod in the southern Chukchi Sea.

Strong linkages between sea ice and Arctic Cod life history suggest that the distribution of Arctic Cod in the southern Chukchi Sea could be influenced by the distribution of sea ice. While Arctic Cod occupies environments that are seasonally ice-free, it is often characterized as a sympagic species for a portion of its life cycle (Craig et al. 1982; Lønne and Gulliksen 1989). Arctic Cod is thought to spawn under sea ice, and buoyant eggs float to the ice-water interface before hatching in early spring (Graham and Hop 1995; Bouchard and Fortier 2011). Sea ice also provides a platform for the growth of sea-ice algae, which is not only an important source of primary productivity in the Arctic, but also has a distinct isotopic signature that can be traced throughout Arctic food webs (Iken et al. 2005; Gradinger 2009). Isotopic analysis has linked Arctic Cod to sea-ice derived carbon, demonstrating the significant influence that sea ice can have on the diet of Arctic Cod (Kohlbach et al. 2017; Dissen et al. 2018). Finally, the seasonal melting of sea ice is a driver of springtime patterns of productivity in the Arctic. Retreating sea ice exposes open water to solar radiation, while freshwater input stabilizes the water column, creating an environment where phytoplankton can bloom (Wang et al. 2005). Ice-edge blooms typically follow the retreat of sea ice, with productivity peaking ~20 days after ice retreat (Perrette et al. 2011). The spring bloom stimulates and supports secondary productivity, ultimately resulting in planktonic food resources for larger vertebrates like Arctic Cod (Sigler et al. 2011; Wassmann and Reigstad 2011).

Given the link between sea ice and Arctic Cod life history, sea ice extent and retreat may influence spring distribution of Arctic Cod in the southern Chukchi Sea. It is possible that Arctic Cod tracks the springtime ice retreat and the wave of productivity that follows. However, in spring of both 2017 and 2018, when sampling occurred, the sea ice edge had already retreated far north of the sampling region (NASA 2018). If Arctic Cod followed the ice edge in these years, then its distribution would be beyond the northernmost station sampled during the June cruises, explaining the extremely low abundances of subadult and adult Arctic Cod observed in the southern Chukchi Sea. It is unlikely that the low abundances of subadult and adult Arctic Cod in the southern Chukchi Sea can be explained by Arctic Cod moving south into the northern Bering

Sea. Arctic Cod is primarily an Arctic species and the northern Bering Sea is at the edge of its geographic range (Mecklenburg et al. 2011). As well, Arctic Cod is found episodically in the northern Bering Sea in association with cold conditions and large ice extent (Wyllie-Echeverria and Wooster 1998; Cui et al. 2009), which did not occur in 2017 or 2018. Furthermore, sampling in the northern Bering Sea from St. Lawrence Island to the Bering Strait caught few Arctic Cod in 2017 and 2018 (Danielson et al. 2018), suggesting that Arctic Cod did not move into the northern Bering Sea

Movement inferred from sized-based and seasonal patterns in distribution describes a plausible migration scenario. In classical fisheries science, the life history of a species that undertakes a migration triangle travels from nursery grounds as juveniles, to feeding grounds as subadults, to spawning grounds upon maturation. The triangle is complete when eggs and larvae are passively transported from the spawning grounds to the nursery grounds via oceanic currents and the cycle begins again (Harden Jones 1968; Secor 2002). Small, young Arctic Cod are most abundant in the northeast Chukchi Sea, perhaps indicating that region functions as nursery grounds for juveniles. The northeast Chukchi Sea was also proposed as a nursery area by researchers analyzing the pelagic distribution of age-0 Arctic Cod, though the suggestion remains untested (De Robertis et al. 2017b). The next step in a migration triangle is the movement of subadults to feeding grounds; in the current study, the distribution pattern of the medium size class was different from the small size class, indicating that medium Arctic Cod move away from areas occupied by small fish and disperse across the productive northeast Chukchi Sea shelf (Grebmeier 2012) to take advantage of feeding opportunities. The final component of a classic migration triangle is movement to spawning grounds; the current study cannot address this directly as Arctic Cod spawns in the late fall and early winter under sea ice (Ponomarenko 2000). Several locations in the northern Bering Sea and near the Chukotka peninsula have been recognized for their potential as Arctic Cod spawning grounds (C. Vestfals, personal communication). Generally, the majority of mature spawners are >100 mm (Nahrgang et al. 2016); in the current study, mature spawners would primarily be in the large size class, which was abundant south of Cape Lisburne during late summer, near the proposed spawning locations (Figure 4). Potential spawners in the southern Chukchi Sea in late summer would not have far to travel to proposed spawning grounds during the fall and winter seasons.

Completion of the proposed migration scenario could be achieved via advection of eggs and larvae by the northbound currents traveling through Bering Strait and across the Chukchi Sea (Weingartner et al. 2005). Pelagic (De Robertis et al. 2017b) and demersal distributions are consistent with northward advection of eggs and larvae from southern spawning grounds. The spring absence of Arctic Cod from the southern Chukchi Sea may be explained within the framework of the proposed migration triangle. In the spring, adult Arctic Cod following the seasonal northward retreat of sea ice may be spawners seeking resources to replenish their depleted energy reserves. Spawning is energetically costly and these individuals would likely need take advantage of the earliest available food resources (Hop et al. 1995). This possible movement scenario synthesizes both size-based and seasonal distribution patterns of Arctic Cod and represents a new effort characterizing Arctic Cod migration patterns in the Chukchi Sea.

The migration of a small-bodied, high-latitude fish species is not unprecedented, but there remains much uncertainty surrounding the migration patterns of Arctic Cod in the Chukchi Sea. Other marine fish species in the North Pacific also exhibit seasonal migrations between feeding grounds and spawning grounds. Pacific Herring in the Bering Sea, for example, exhibit a clockwise seasonal migration between spawning grounds near the Alaskan coast, feeding grounds offshore on the Bering Sea shelf, and overwintering grounds near the Pribilof Islands (Tojo et al. 2007). In the eastern Bering Sea, Walleye Pollock that are $\leq$50 cm undertake a northward and shoreward summer feeding migration in response to warming water temperatures (Kotwicki et al. 2005). Additionally, telemetry studies in the Atlantic Arctic found that Arctic Cod is capable of traveling over 100 km in response to rapidly evolving ice conditions (Kessel et al. 2015). The migration triangle proposed here is not yet complete, as it is limited to spring and summer open water sampling efforts. Though logistically challenging, it is necessary to confirm or refine the sequence of Arctic Cod movements in the Chukchi Sea with observations from the ice-covered season. Moored acoustics offer an opportunity to detect Arctic Cod movement during the Arctic winter. Acoustic sensors on moorings are deployed and recovered during ice-free periods, but collect data throughout the winter; patterns in backscatter provide information on fish presence and abundance during the ice-covered season, when net sampling is not possible (Kaartvedt et al. 2009). Moored acoustic technology has already proven useful for high-latitude research, where it has been used to detect aggregations of under-ice zooplankton and nekton (Brierley et al. 2006; La et al. 2015), and is emerging as a viable technique for estimates of fish abundance (De Robertis et al. 2018). The scale of detail of the migration triangle proposed here is coarse, but nevertheless provides an initial framework against which new information may be tested to advance understanding of Arctic Cod movement patterns in the Chukchi Sea.

Conclusions

Advancing fisheries science in the remote and inaccessible Arctic ecosystem is a significant research challenge. The work presented here compiles a large number of disparate individual sampling efforts to develop a holistic picture describing Arctic Cod summer distribution in the Chukchi and Beaufort seas. The size-based analysis demonstrates ontogenetic shifts in distribution, while consideration of environmental covariates provides insight into potential mechanisms driving these patterns. Though much work remains to be done in understanding Arctic Cod distribution and migration, the comparison between spring and summer abundances shows that Arctic Cod distribution in the Pacific Arctic varies by season and suggests that this species may undertake some form of seasonal migration. The mapping of Arctic Cod distribution in the Chukchi and Beaufort seas improves understanding of one of the most abundant and critical trophic links in the Arctic ecosystem. As the Arctic experiences increased anthropogenic and climatological pressures, thorough knowledge of key components of this system, including species like Arctic Cod, will inform responsible decision making in this dynamic and rapidly changing ecosystem.

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Appendix

IACUC Approval

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UNIVERSITY OF ALASKA FAIRBANKS

Institutional Animal Care and Use Committee

909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

May 15, 2017

To:	Brenda Norcross, MS, PhD Principal Investigator
From:	University of Alaska Fairbanks IACUC
Re:	[1054017-4] Offshore Arctic Fish Sampling

The IACUC reviewed and approved the Personnel List referenced above by Administrative Review.

Received:	May 12, 2017
Approval Date:	May 15, 2017
Initial Approval Date:	May 15, 2017
Expiration Date:	May 15, 2018

This action is included on the June 8, 2017 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*

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UNIVERSITY OF ALASKA FAIRBANKS

Institutional Animal Care and Use Committee

909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

March 12, 2018

To:	Brenda Norcross, MS, PhD Principal Investigator
From:	University of Alaska Fairbanks IACUC
Re:	[1054017-5] Offshore Arctic Fish Sampling

The IACUC has reviewed the Progress Report by Designated Member Review and the Protocol has been approved for an additional year.

Received:	March 3, 2018
Initial Approval Date:	May 15, 2017
Effective Date:	March 8, 2018
Expiration Date:	May 15, 2019

This action is included on the March 8, 2018 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures detailed in the form 005 "Reporting Concerns".*